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Distributional ecology of red-capped plover, *Charadrius ruficapillus* (Temminck, 1822), on Western Australian salt lakes

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Abstract. Red-capped plovers, *Charadrius ruficapillus* (Temminck, 1822), were censused by day during the breeding season in thirty plots along the shore of a salt lake in the south-west of Western Australia. Multiple regression analysis showed that food and habitat variables accounted for 63.4% of the total variation in bird numbers between plots, whereas principal components regression explained 59.2% of the variation. The major predictors of bird numbers were the width and slope of the shore and the orientation of the plots. These variables probably reflect the ease with which birds can exploit terrestrial prey such as ants, and aquatic prey such as dytiscid beetles, which constitute the principal food of *C. ruficapillus*. Bird numbers were correlated only weakly with the biomass of benthic invertebrates, probably because these prey are most active, and accessible, by night. Numbers of birds were accurately predicted by the multiple regression model at an additional six salt lakes in the south-west of Western Australia. We suggest that regression models may be generally applicable in distributional studies of birds on salt lakes, and in predicting bird numbers in other comparably simple environments.

Key words. *Charadrius,* regression models, salt lakes, waders.

INTRODUCTION

Salt lakes are often considered to be relatively simple, discrete ecosystems, which support impoverished communities of plants and invertebrate animals (Larsen, 1980). However, salt lakes are often exploited by large numbers of wading birds (Aves: Charadrii), and may constitute important seasonal or year-round habitats for many species (Cale, 1984; Saunders & de Rebeira, 1986).

The factors which determine population density of waders on salt lakes are poorly known. At Lake Eyre in South Australia, for example, the highest numbers of red-capped plovers *Charadrius ruficapillus* (Temminck, 1822) occur in shallows with gentle gradients (Blakers, Davies & Reilly, 1984), perhaps because food is easily accessible there. On Rottnest Island in Western Australia, populations of several species of waders are distributed unevenly around salt lakes in apparent response to the patchy distribution of prey organisms (Cale, 1984; Saunders & de Rebeira, 1986). As with most studies of waders on salt lakes, those carried out in coastal bays and estuaries have dealt usually with populations outside the time of breeding. Here, several studies have established simple correlations between wader numbers and prey densities (Wolff, 1969; Goss-Custard, 1970a; Goss-Custard, Kay & Blindell, 1977; Baird *et al.,* 1985), or indirect correlations between wader numbers, prey and type of substrate (Bryant, 1979; Hicklin & Smith, 1984). Wader numbers are probably also influenced locally by habitat, the presence of competitor species, climatic and environmental conditions (Pienkowski, 1981), but the relative importance of these several variables in determining abundance has not been assessed for any species.

The present study aims to: (i) investigate the distribution, at breeding time, of one species of wader, the red-capped plover *Charadrius ruficapillus,* along the shore of a salt lake in Western Australia; (ii) derive a predictive model of plover numbers from an array of biotic and abiotic variables; and (iii) assess whether the model can be used to predict plover numbers during the breeding period at other, geographically discrete salt lakes in Western Australia.

THE STUDY ORGANISM

Charadrius ruficapillus (Fig. 1) is widespread on salt lakes and in coastal areas of southern Australia, and was the most abundant species of wader encountered in the present study. Numbers are usually highest and most stable in spring and summer, and lowest in winter due to emigration (Saunders & de Rebeira, 1986). *Charadrius ruficapillus* is largely insectivorous (Poore, Corrick & Norman, 1979). Four males killed during the present study had dytiscid beetles, ants and possibly polychaete worms *Capitella capitata* (Fabricius, 1780) in their guts (Abensperg-Traun,

FIG. 1. Red-capped plover, *Charadrius ruficapillus* (Temminck, 1822). Photo by M. K. Morcombe.

1986), suggesting that foraging occurs largely on the littoral fringe. Birds pair and produce a single clutch of two eggs during the summer (Hobbs, 1972); there is no evidence of group nesting.

STUDY AREAS

Initial census data to derive a predictive model were gathered at Lake Preston, a coastal hypersaline lake between Bunbury and Mandurah in the south-west of Western Australia (Fig. 2). The lake is 27 km long, up to 2 km wide, with a minimum water surface of ~4000 ha during the summer. The lake is maintained by direct rainfall accession and inflow of hypersaline groundwater (Commander, 1984), and attains a maximum salinity of 367‰ (total dissolved solids) in the northern sector and 78‰ in the south (Moore, 1987). Sparse halophytic herbs such as *Polypogon monspeliensis* L. (Desf. 1798), *Salicornia quinquiflora* (Ung.-Sternb. A. J. Scott, 1977), *Juncus kraussii* (Hochst, 1845) and *Lawrencia glomerata* (Hook, 1842) dot the littoral fringe, and grade into *Melaleuca* spp. and *Eucalyptus* spp. at the treeline (Fox, Downes & Maslin, 1980). The lake experiences a mediterranean climate, with most of the annual rainfall of ~880 mm falling in winter (June–August). Daytime temperature maxima in summer are 25–35°C.

Further census data to test the predictive model were collected at Lakes Clifton, Pollard, Newnham and Martins Tank at least 3 km to the north and east of Lake Preston,

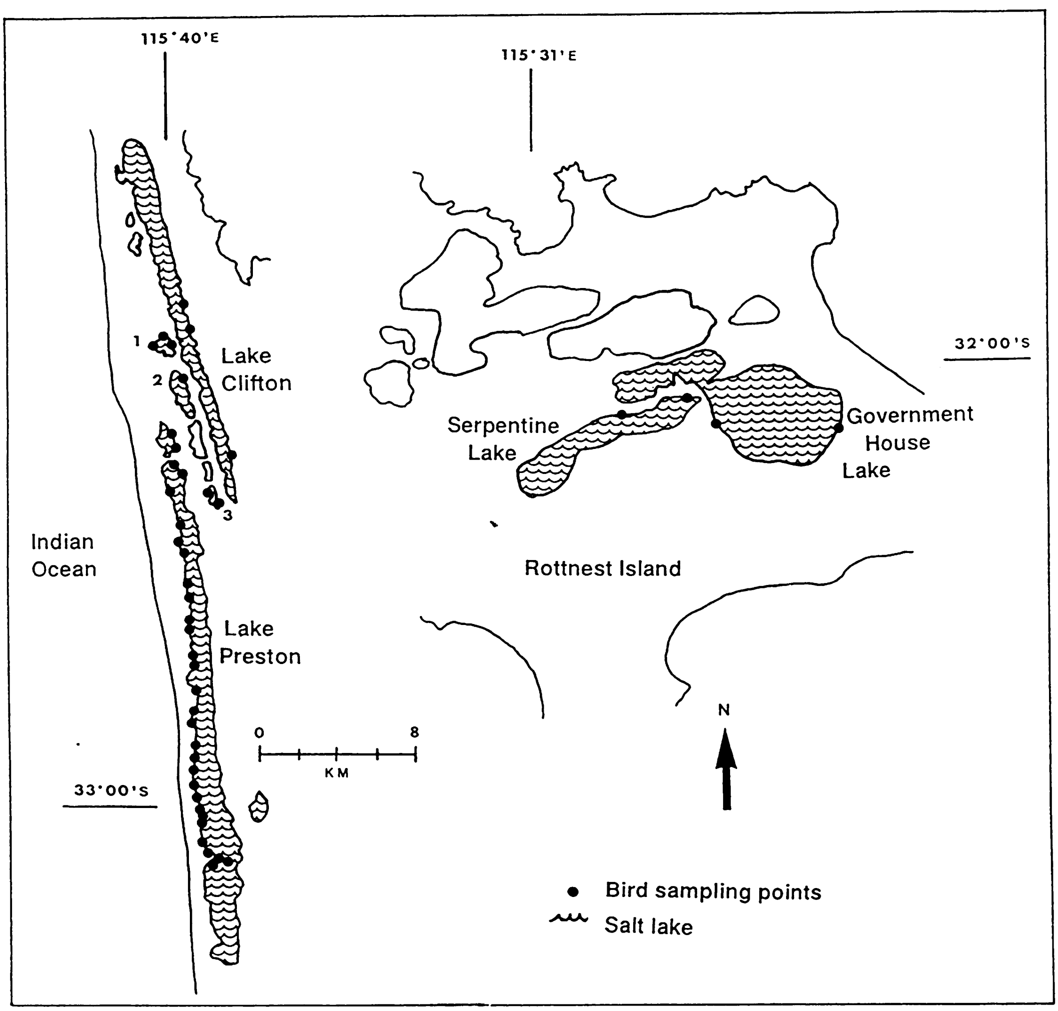

FIG. 2. Study areas showing sampling plots (•). 1=Lake Pollard, 2=Martins Tank, 3=Lake Newnham.

and at Government House Lake and Serpentine Lake on Rottnest Island, 100 km to the north (Fig. 2). These lakes experience generally similar climatic regimes, but differ in salinity, ionic concentrations and in the composition of invertebrate communities (Hodgkin, Sanders & Stanley, 1979; Edward, 1983; Moore, Knott & Stanley, 1983).

MATERIALS AND METHODS

The following methods were used to derive data for a predictive model of plover abundance.

Sampling plots and bird counts

Data were collected in thirty plots measuring 150×25 m, set at random locations mostly on the western shore of Lake Preston (Fig. 2). Plots were positioned along the waterline, with 750 m^2 of plot area in the shallow nearshore zone and the remaining 3000 m^2 occupying the terrestrial fringe. Plot size was constrained by the ease with which reliable bird counts could be made (Goss-Custard, 1977). Each plot was censused for birds eight times over a period of 4 days, four times in the mornings and four in the afternoons. The time and sequence of censuses was randomized at each plot, with each census lasting 15 min (Grant, 1981). All plots were censused over a 3-week period between 26 December 1985 and 18 January 1986 when *C. ruficapillus* was nesting, to minimize variation in bird numbers due to seasonal changes or movements.

Environmental variables

Fourteen biotic and abiotic variables were measured.

Food. Thirty 100 cm^3 sediment samples were removed from along the waterline in each plot to sample potential prey. Samples were taken to a depth of 5 cm, and sieved through 1 mm mesh to collect invertebrates (Bengtsen & Svensson, 1968; Thomas & Dartnall, 1971; Evans & Dugan, 1984). Sampling was carried out by day to coincide when birds were observed foraging. This procedure yielded representative samples of polychaete worms, but not of other potential prey. For each plot, mean worm numbers, mean dry biomass (g), and the coefficients of variation associated with the means, were calculated. Worms were dried at 60°C to constant weight to obtain dry biomass.

Sediment particle size. Two 100 cm^3 sediment samples were removed from along the waterline in each plot, dried at 50°C for 48 h, and weighed. The samples were then placed in an Endecott test sieve shaker and sieved for 15 min to obtain the following three particle size components (after Folk, 1974): *coarse* (gravel, ⩾2.0 mm diameter), *medium* (sand, ⩾0.063 mm <2.00 mm diameter) and *fine* (silt and mud, <0.063 mm diameter). Each size component was weighed, and the contribution of that component to the original dry sample weight expressed as a percentage.

Salinity. Fifteen surface water samples were removed 2 m from the shore in each plot, and conductivity determined in the laboratory using a WPA CM25 Conductivity Meter. Conductivity was calculated using the equation

$$EC_{25} = G \times k \times f_t$$

where EC_{25} is conductivity at 25°C, G is conductance (meter reading), k is a cell constant (0.74) and f_t is a temperature correction. The EC_{25} value was plotted on a calibration curve to establish salinity in parts per thousand of total dissolved solids (Avery & Bascomb, 1974).

Slope of shore. Water depth (cm) at 5 m from the waterline was determined at fifteen stations within each plot, and the mean used as an index of the slope of the shore.

Width of shore. This was calculated as the mean of three measurements of the distance (m) from the waterline to the treeline in each plot.

Plot orientation. This was the compass orientation of a line drawn perpendicular to the waterline in the centre of each plot, taken in the direction of the lake.

Groundcover. The mean percentages of terrestrial plant and surface rock cover were established from sixty 1 m^2 quadrats taken in the terrestrial portion of each plot; percentage cover of aquatic rock was measured similarly in plots below the water line.

Statistical methods and tests of the model

Preliminary inspection of the matrix of environmental variables revealed that some pairs of variables were highly correlated. To reduce the multicollinearity, we regressed each environmental variable on combinations of all the others, and rejected those with overall R^2 values of ⩾93% (Beale, Kendall & Mann, 1967; Kendall, 1980). The rejected variables were salinity, medium and coarse sediment, and the coefficients of variation of worm numbers and biomass. A principal components analysis on the correlation matrix showed further that these variables were associated with small eigenvalues (<1.1), and hence confirmed their minimal contribution (10.5%) to variance in the original data matrix. These procedures left only six statistically significant correlation coefficients ($P<0.05$) among the thirty-six pairwise combinations of variables in the remaining data matrix.

Simple linear regressions were run of mean bird numbers per plot against each of the environmental variables. After analysis of the residuals, the following transformations were made to improve linearity: mean bird numbers, ($\log_{10}[x+1]$); mean worm numbers and biomass, ($\log_{10}$); percentage fine sediment, aquatic, terrestrial rock and terrestrial plant, (arcsine). Stepwise multiple linear regression analyses were used next to generate a predictive model of bird abundance, using mean transformed bird numbers per plot as the dependent variable and the environmental parameters as independent variables. Both step-up and step-down models produced similar results; only data from the step-up analyses are presented here. The data matrix was further analysed in a principal components regression, using uncorrelated factor scores generated from the original environmental parameters as new independent variables (Montgomery & Peck, 1982). Computations were carried out using SPSS regression and factor analysis routines.

Bird numbers, and variables identified in the multiple regression model as significant predictors of bird numbers, were measured as described above on thirteen plots at the six test lakes between 16 February and 10 March 1987. As at Lake Preston, these censuses were carried out when birds were nesting. The fit of the observed with the predicted number of birds on each plot is presented graphically, and accepted if the actual number falls within 1 SE of the prediction estimate.

RESULTS

C. ruficapillus at Lake Preston

Mean plover numbers varied between 0 and 19.4 per plot over the entire period of study. Variation in numbers within plots during the census period was less marked than the variation between plots, with the highest mean counts per plot, recorded in the first and last censuses, being only double the lowest count recorded in census 4 (Fig. 3).

Mean transformed plover numbers were correlated with width of shore ($r=+0.69$, $P<0.001$), plot orientation ($r=+0.51$, $P<0.01$), and slope of shore ($r=-0.53$, $P<0.01$), but not with other variables (Fig. 4). These variables were also included in a multiple regression model with one food variable, the mean number of benthic worms per plot (Table 1). The equation

$Y=-0.0147+0.0066$ (SE 0.0019) (width of shore)$+0.0113$ (SE 0.0075) (slope of shore)$+0.2877$ (SE 0.1238) (mean worm numbers)$+0.0017$ (SE 0.0008) (plot orientation)

produced a good fit to the data, accounting for 63.4% of the variation in plover numbers ($F=10.85$, $P<0.001$).

The first three factors extracted in the principal components analysis accounted for 71% of the variation in the original variables. A multiple regression using these factors as new independent variables yielded the equation

$Y=0.677+0.249$ (SE 0.044) (Factor 2)-0.123 (SE 0.044) (Factor 3)

with progressive R^2 (%) values of 47.5% and 59.2% ($F=19.56$, $P<0.001$). Bird numbers were correlated positively with Factor 2 ($r=+0.59$, $P<0.001$) and negatively with Factor 3 ($r=-0.37$, $P<0.05$), but not at all with Factor 1 ($r=0.04$, P n.s.). Factors 2 and 3 can be interpreted as abiotic components of the environment, representing primarily the width and slope of the shore, plot orientation, and the percentage of aquatic or terrestrial rock within plots (Table 2). In contrast, Factor 1 can be interpreted as a food variable, with high factor loadings on both mean worm numbers and worm biomass (Table 2).

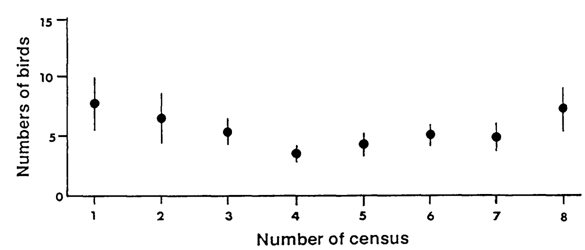

FIG. 3. Numbers of *C. ruficapillus* (Temminck, 1822) ($\bar{x}\pm$SE) observed over the course of eight censuses in thirty study plots at Lake Preston, Western Australia.

TABLE 1. Summary of stepwise multiple regression analysis of mean transformed plover numbers on environmental variables.

Step variable	Standard partial regression coefficient	Multiple correlation coefficient	Incremental R^2	R^2 for variables	F for variables	P
1. Width of shore	+0.499	0.69	0.48	0.48	25.39	<0.001
2. Slope of shore	−0.208	0.73	0.54	0.06	3.55	0.070
3. Mean worm numbers	+0.314	0.76	0.58	0.04	2.42	0.132
4. Plot orientation	+0.316	0.80	0.63	0.06	4.01	0.056

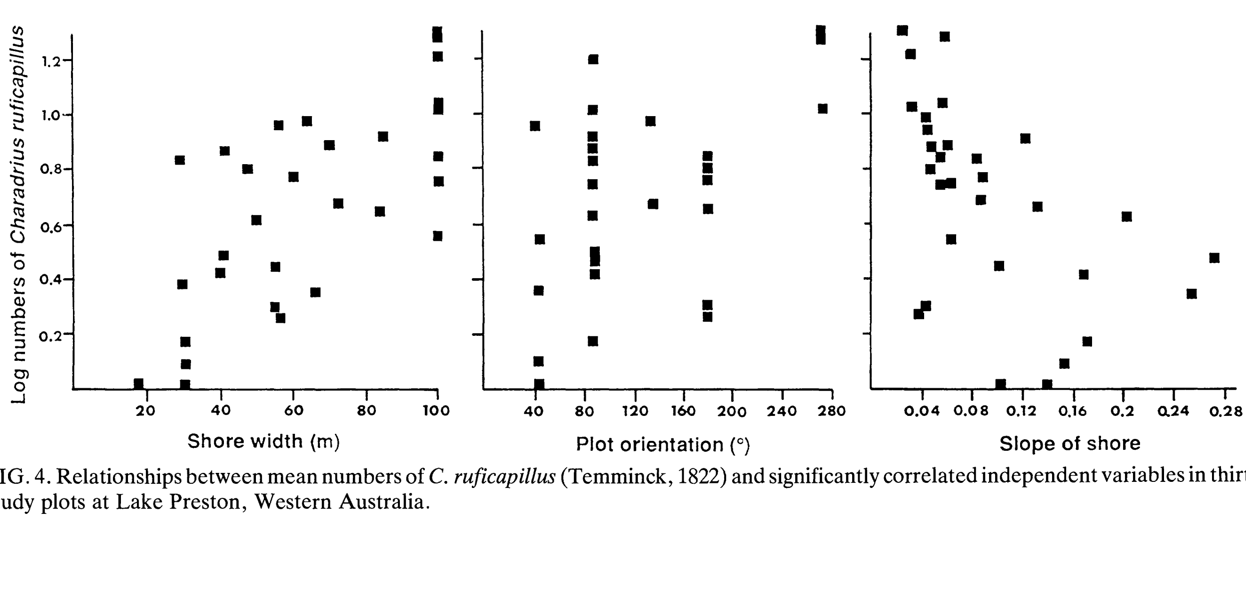

FIG. 4. Relationships between mean numbers of *C. ruficapillus* (Temminck, 1822) and significantly correlated independent variables in thirty study plots at Lake Preston, Western Australia.

TABLE 2. Significant loadings of environmental variables on principal components used in the multiple regression analysis.

Variables	Principal components		
	1	2	3
Mean worm numbers	+0.90		
Mean worm biomass	+0.89		
Fine sediment	−0.61		−0.48
Slope of shore			+0.79
Width of shore		+0.84	
Plot orientation	−0.46	+0.60	
Terrestrial rock		+0.72	
Aquatic rock			+0.76
Terrestrial plants			+0.64

C. ruficapillus at other salt lakes

Mean plover numbers at the six additional salt lakes varied from 0.5 to 16.5 per plot. The transformed values were again correlated with width of shore ($r=+0.72$, $P<0.01$), plot orientation ($r=+0.57$, $P<0.05$) and slope of shore ($r=-0.60$, $P<0.05$) but not with other variables. The numbers of birds were accurately predicted by the multiple regression model using the original independent variables at twelve of the thirteen plots (Fig. 5). Underestimation of the actual numbers occurred in one plot, at Lake Clifton, where abundant flying insects may have provided an additional source of food for the plovers.

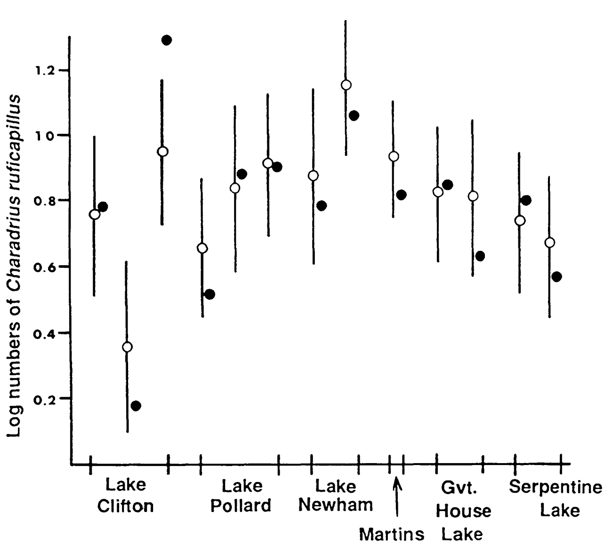

FIG. 5. Actual (●) and predicted (○) numbers of *C. ruficapillus* (Temminck, 1822) at six salt lakes in Western Australia. Predicted numbers are shown ±SE.

DISCUSSION

The regression models consistently identified abiotic variables as major predictors of plover numbers at the seven salt lakes investigated in this study. This finding accords with the observation by Blakers *et al.* (1984) that *C. ruficapillus* favours shallow near shore zones on salt lakes, but apparently conflicts with the majority of studies on waders which suggest that food is the major determinant of abundance. We will first review the reliability of our bird census data, then consider the direct biological relevance of abiotic variables to *C. ruficapillus,* and finally suggest that these variables are themselves predictors of food availability.

Three observations suggest that our counts of *C. ruficapillus* were reliable. First, the birds were always visible and easily counted within plots due to the open nature of the habitat. Second, birds did not appear to be disturbed by our presence. Although a decline in numbers on each plot occurred between the first and fourth censuses, numbers usually returned to initial levels by the time of the final census (Fig. 3). The decline may have reflected the proportion of young or non-breeding individuals within each plot that were not strongly site-attached; the increase in numbers in later censuses may have been due to birds becoming accustomed to the presence of the observers. Third, individuals of both sexes usually remained in the vicinity of their nests throughout the period of study, even if disturbed by occasional vehicle noise or the presence of larger animals near the plots, such as cattle and emus. Few individuals are therefore likely to have been represented in counts on more than one plot, confirming that within-plot censuses should be both independent and reliable.

Given that many species of waders are territorial and often evenly dispersed during the nesting period (Simmons, 1956; Holmes, 1966, 1970; Pienkowski, 1984), the relatively large variation in numbers of *C. ruficapillus* between our study plots was unexpected. Although territorial behaviour has apparently not been documented in this species, several observations of agonistic interactions between neighbouring birds suggest that territoriality may indeed occur. If plovers were defending territories at the time of the study, it is possible that the most densely populated plots had increased numbers of surplus, non-breeding individuals that were tolerated by the breeding pairs.

Increased numbers of *C. ruficapillus* in plots with wide and gently sloping shorelines may be a consequence, in part, of the improved chance for individuals of detecting the approach of terrestrial predators such as foxes (*Vulpes vulpes* (L.)), cats (*Felis catus* (L.)) and goannas (*Varanus gouldii* (Gray, 1838)). However, our observations suggest that birds typically take flight at ~15 m when approached by humans; this distance is less than the minimum distance from the treeline to the shoreline measured in the thirty plots at Lake Preston. Moreover, we have no direct evidence that *C. ruficapillus* forms a significant part of the diet of terrestrial predators at any of the salt lakes: no remains of Charadrii have been found in twenty-four fox droppings collected from Lake Preston or in thirty-two cat droppings from Rottnest Island; sightings of these predators are also rare (C.R.D. and M.A.-T., personal observations). Frauca (1967) found no evidence of eggs or chicks of *C. ruficapillus* being destroyed by terrestrial predators, and suggested that their cryptic coloration provided efficient camouflage. Thus, while heavy predation has been documented on wader clutches elsewhere (Larsen, 1960; Page *et al.*, 1983; Pienkowski, 1984), it is unlikely to have been substantial in the present study and is not an obvious immediate explanation for the increased numbers of plovers on wide shores. Unfortunately, rigorous experimental tests to precisely determine the effects of predation on clutches or adult birds were beyond the scope of the present study.

Although abiotic characteristics of the shoreline and littoral fringe have little obvious biological relevance for *C. ruficapillus,* they may facilitate access of birds to invertebrate food resources. Thus, a wide shore may be important in increasing foraging area and thus access to terrestrial invertebrates such as ants (Corrick & Cowling, 1975). A gentle shoreline should similarly provide greater access to aquatic prey and, as the water level recedes due to evaporation over the summer, may expose fresh sediments and prey populations at a relatively high rate. A positive correlation of bird numbers with plot orientation may also be explained by reference to food resources. Thus, plots facing the predominant westerly and south-westerly sea breezes were more likely to receive wind-blown invertebrates than east-facing plots; such prey were also more likely to be trapped and taken by birds from the abundant, sticky, saline foam (see also Cale, 1984). Previous studies have shown that exposure to wind is likely to adversely affect nesting success (Mayfield, 1961). However, in the present study the highest bird numbers occurred in plots that were most exposed to wind; moreover, all plots were probably exposed equally to insolation. Further circumstantial evidence of the importance of food as a predictor of bird numbers was obtained in two plots at the northern end of Lake Preston. An average of 19.4 *C. ruficapillus* per plot occurred here early in the study when chironomid pupae were abundant; numbers declined to zero within 2 weeks when all pupae disappeared (Abensperg-Traun, 1986).

If food resources are important for *C. ruficapillus,* why were bird numbers not correlated directly with our food variables? Plovers take prey from the terrestrial and aquatic environments, but our invertebrate samples comprised mostly the benthic polychaete *Capitella capitata.* The importance of *C. capitata* in the diet of *C. ruficapillus* is not known. However, the small size of this species (mean dry weight per worm 0.002 g) may mean that it is passed over in favour of more easily detectable and energetically profitable prey such as ants (Goss-Custard, 1977; Myers, Williams & Pitelka, 1979), which were recovered infrequently by our sampling methods. Furthermore, observations by R. J. Cunningham (personal communication) at Lake Newnham indicate that other potential prey, such as dytiscid beetles, move into deep water by day and return to the shallows by night. Birds would be able to exploit these prey at night (Dugan, 1981), and could moreover be expected to maximize their energetic returns by foraging in gently sloping parts of the near-shore zone where prey numbers would be highest and escape to deeper waters most difficult. Plovers forage almost entirely by visual means, catching, for instance, benthic invertebrate prey by exploiting brief periods of surface activity aimed at respiration or food procurement (Goss-Custard, 1970b; Baker & Baker, 1973; Pienkowski, 1983). As burrowing is energetically expensive, it would be advantageous for benthic prey to remain as close to the surface as conditions of temperature and predation allow, and to keep visits to the surface as brief and infrequent as possible. Our sampling frequency and depth of 5 cm may have thus been inadequate to detect all the benthic invertebrates available to *C. ruficapillus.*

Most previous attempts to predict bird numbers using multiple regression models have yielded unreliable results, either because inappropriate independent variables have been measured, or because the parameters built into the models have been site-specific and cannot validly be used in other areas (Wiens & Rotenberry, 1981; Maurer, 1986). In contrast, the variables selected in the present study accounted for a relatively high proportion of the variation in numbers of *C. ruficapillus,* and reliably predicted numbers at an additional six lakes. The success of our regression model probably reflects the structural and biotic simplicity of salt lake environments, in that relevant independent variables can be easily identified and measured. In addition, the structural and biotic similarities between salt lakes probably allowed valid extrapolation of the model parameters. We conclude that regression models may have general applicability in distributional studies of salt lake birds, and suggest that the use of such models could usefully be extended to other, comparably simple environments.

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